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Global motion adaptation

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Abstract

Image motion is initially detected locally. Local motion signals are then integrated across space in order to specify the global motion of objects or surfaces. It is well known that prolonged exposure to motion causes adaptation at the local motion level. We have investigated whether adaptation also occurs at the global motion level. We have devised a global motion stimulus (a random dot kinematogram) which has equal motion energy in opposite directions but nonetheless gives rise to global motion perception. At the local motion level, adaptation to this stimulus should cause equal adaptation in both directions and should not give rise to an aftereffect. Any aftereffect seen must therefore be attributable to adaptation at the global motion level. We find that following adaptation to this stimulus, judgements of the perceived direction of a test pattern are systematically biased towards the direction opposite to the adapting direction, suggesting that adaptation does occur at a level of visual processing at which global motion is represented.

Keywords: Motion; Global motion; Motion aftereffect; Adaptation; Kinomatogram

1. Introduction

Adaptation studies have been used widely in visual psychophysics as a means of identifying the various components, channels and sub-systems that make up the visual system. The general rationale is that adaptation to a given visual stimulus will tend to cause habituation in those neurones that are responsive to it and the perception of a subsequently viewed visual stimulus may then be altered in a way that reveals the stimulus specificity of the adapted neurones (Barlow & Hill, 1963; Maffei, Fiorentini & Bisti, 1973; Vautin & Berkley, 1977). The perception of a test stimulus that is processed independently of the adapting stimulus will be unaffected by adaptation. Where a perceptual aftereffect of adaptation is observed, the magnitude of the effect indicates the degree of common processing between the adaptation and test stimuli.

Adaptation to motion reveals the existence in human vision of mechanisms that are selective for the direction of moving stimuli (e.g. Wohlgemuth, 1911; Sekuler & Ganz, 1963; Tolhurst, 1973; Nakayama, 1985). However, adaptation studies have not fully addressed a fundamental distinction that now pervades the motion literature, that between local motion and global motion. It is widely accepted that image motion is initially detected locally, giving rise to a large array of motion vectors at different image locations. These local motion signals are subsequently integrated across space into regions that share a common velocity, giving a percept of global motion (Williams & Sekuler, 1984; Newsome & Paré, 1988).

Adaptation to motion takes place at least partly at the local motion level. Motion after-effects are typically confined to the adapted region of the visual field, suggesting a local effect, and physiological adaptation is well documented in the primary visual cortex, where motion signals are of the local variety. However, it has been suggested that adaptation may also occur after, as well as before, global motion integration. For example Blake (1995) has shown that presenting an adaptation pattern during binocular rivalry suppression weakens the aftereffect of adaptation to spiral motion, even

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though it does not weaken the affect of adaptation to simple translational motion (Lehmkuhle & Fox, 1975). This suggests two stages of adaptation, one early and based on local motion vectors, the other occurring later, after the site of rivalry and at a stage where more complex motions are encoded.

Several other previous studies are consistent with adaptation at the global motion level. Blake and Hiris (1993) showed that the motion aftereffect (MAE) can be nulled by global motion of the type introduced by Newsome and Paré (1988), in which dots moving in a common signal direction are embedded in noise dots. This might reflect nulling of adaptation at the global motion level. However, since every location in the image will, averaged over time, receive motion stimulation that is biased in the nulling direction, it could just as well reflect nulling of a local motion aftereffect at every location. Raymond (1993) showed that adaptation to motion causes threshold elevation in terms of the signal/noise ratio of a Newsome and Paré stimulus and that 100% interocular transfer of the elevation occurs. This is also consistent with adaptation in neurones beyond the level at which local motion signals are integrated across space. But, again, this interpretation is not logically necessary. Adaptation may simply weaken the magnitude of the local signals that feed into the global motion process, so that more signal dots must be added in order to compensate. Bex, Metha and Makous (1999) have recently reported that adaptation to four motion patches arranged around a fixation point results in greater adaptation when the patches are consistent with a gobal rotation or expansion pattern than when configured as global translation, and they invoke the existence of local and global processing stages to explain the difference. This evidence of global adaptation is suggestive, but again indirect.

Several psychophysical studies have identified two different after-effects of motion which may be associated with different processing stages. Ashida and Osaka (1994) noted that the motion aftereffect is more broadly tuned for spatial frequency if a counterphased test grating is used in place of a static grating and concluded that two different mechanisms are at play. Nishida and Sato (1995) found that adaptation to second-order motion gives rise to a motion aftereffect when a dynamic test pattern is used but not with a static test pattern and, again, argued that static and dynamic test patterns reveal two different types of adaptation. Greater interocular transfer occurs when a dynamic test pattern is used (Nishida, Ashida & Sato, 1994), suggesting that the aftereffect may reflect a processing stage further removed from the retina than that revealed by the use of a static test pattern. The interpretation of these studies has focused on the distinction between first- and second-order motion, rather than that between local motion and global motion. Since one is thought to occur at a higher level than the other, it is possible that the two adaptation effects might reflect processing at local and global motion levels, but at present there is no direct evidence for such an interpretation. The dynamic motion aftereffect cannot therefore be seen as a demonstration of adaptation at the global motion level.

A related line of study involves simultaneous adaptation to two motion directions. If two directions are either alternated (Riggs & Day, 1980) or viewed transparently (Verstraten, Fredericksen & van de Grind, 1994) during adaptation, the resulting MAE has a single direction corresponding to that opposite to the vector sum of the adapting directions. This might reflect adaptation at a level where directions have been integrated. But, as with the study of Blake and Hiris (1993), it is possible that the phenomenon simply reflects the average adaptation at the local level. Verstraten, van der Smagt, Fredericksen and van de Grind (1999) found that for a static test pattern, the MAE direction resulting from such adaptation reflects the adaptation directions but not their speeds, while a dynamic test pattern yields an MAE direction that depends on both the directions and speeds of the two adaptation components. This confirms the existence of two levels of adaptation as discussed above and shows that both produce a single MAE direction related to the vector sum.

In summary, there is substantial evidence for the existence of at least two levels of motion adaptation in the visual system, but it is not at all clear what the key functional difference(s) between the two might be (local versus global, first-order versus second-order, fast versus slow, etc.). In this study we explored a new approach to establishing whether adaptation to motion can occur at a level of processing at which global motion is represented. An adaptation stimulus is devised in which local motion is equal in opposite directions, so that no net motion adaptation will arise in local motion sensors, and yet global motion is perceived in a single direction. Following exposure to this stimulus, direction judgements of a test pattern are biased in the direction opposite that of the global motion in the adaptation pattern, suggesting that true global motion adaptation does indeed occur.

2. Experiment 1

The strategy used to isolate adaptation at the global motion level exploits the fact that when opposite directions of motion are alternated during the adaptation period, no aftereffect of motion is observed. This is because motion adaptation, although it still occurs, is equal in opposite directions.

The stimuli were random-dot kinematograms (RDKs) of a type similar to those introduced by Newsome and Paré (1988). Each frame contains many dots. On each update, each dot is assigned to be either signal or noise. All signal dots move in a common direction; noise dots move in random directions. Provided the proportion of signal dots exceeds some threshold value (typically 5–10%), global motion is perceived in the signal direction.

During adaptation, two RDKs were alternated. One had a signal-to-noise ratio such that global motion was clearly visible (say rightward). The other had the same number of signal dots, which now moved in the opposite direction (leftward). But the number of noise dots was now much greater, such that the stimulus was below the global motion threshold and no global motion was perceived. When averaged over time, local motion energy is equal in the two opposite signal directions but global motion is perceived in a single direction. Any aftereffect of adaptation involving illusory perception of motion in a directionally ambiguous test pattern (e.g. dynamic noise) must presumably reflect adaptation in neurones (or neurone ensembles) that represent global motion.

In initial experiments, the two stimuli were alternated every 2 s. However, strong adaptation-order effects were obtained. Perceived motion in a directionally ambiguous test pattern was consistently seen in the direction opposite to the most-recently presented signal direction. This confirms the presence (indeed, dominance) of local motion adaptation, since even local motion that was not detectable because of noise dots caused an aftereffect and this aftereffect was strong enough to counteract any adaptation at the global motion level that might also have occurred. But it destroys the rationale of the experiment, since it means that local motion adaptation cannot be assumed to be equal in both directions. The frequency of alternation was increased in an attempt to eliminate adaptation-order effects, but even quite rapid (2 Hz) alternation resulted in measurable order effects for a brief test pattern presented immediately after adaptation. The eventual solution was to alternate the two adaptation phases on a frame-by-frame basis, too fast to be followed visually, as described in Section 2.2.

2.1. Subjects

There were two observers. NSS is one of the authors, IES is an experienced observer who was unaware of the purpose of the experiment.

2.2. Stimuli

The stimuli were RDKs generated and displayed on an Apple Macintosh 7500 computer. All stimuli consisted of a number of white dots of diameter 10 min arc on a grey background (50% contrast) in a circular area of the screen subtending 5° diameter. The positions of the dots were updated at a rate of 37.5 Hz (every two video frames) to produce kinematograms.

The adaptation stimulus consisted of a four-frame sequence repeated many times. Three versions were used, referred to as rightward, leftward and balanced. In all three cases, there were 25 signal dots and a variable number of noise dots. Both signal and noise dots moved with a step size of 11 minarc, which would correspond to a speed of 7°/s if sustained. Signal dots all moved in the same direction; noise dots moved the same distance but in random directions. In the rightward adaptation case, the first frame contained 47 dots, randomly positioned. On the second frame, 25 of the dots (the signal dots, chosen at random) moved rightward while the remainder moved randomly. On the third frame, the 47 dots remained stationary and 203 new dots appeared at random positions, giving a total of 250 dots. On the fourth frame, 25 signal dots (re-selected at random from the 250 dots) moved leftward while the remainder moved in random directions. On the fifth frame, 203 dots (chosen at random) disappeared and the rest remained stationary, leaving 47 dots as in frame one. This cycle repeated continuously for 150 frames (4 s) and the 4-s animation could be repeated to give longer adaptation periods. The result is that during adaptation the display switched rapidly and repeatedly between highly visible rightward global motion and barely visible leftward global motion, with equal motion energy in the two opposite directions along the axis of motion. The appearance of the adaptation stimulus was weak but continuous rightward global motion.

The leftward adaptation pattern was the same as the rightward but with left and right signal directions reversed to give the appearance of leftward global motion. The balanced stimulus had 225 dots in both rightward and leftward phases, of which 22 were signal dots (10% coherence in both directions). It had the appearance of direction noise.

The test pattern was a more conventional global motion pattern. It contained 100 dots in every frame, of which some were signal dots and the remainder noise. The signal dots all moved in the same direction, which could be either rightward or leftward. The proportion of signal dots was constant throughout each such sequence and their direction was invariant. Each test trial lasted for 16 frames (0.43 s). The signal dots were chosen afresh on every update so that the signal dots had a two-frame lifetime, as in the adaptation stimulus. This ensured that their direction could not be determined by integrating over time rather than space. The set of test patterns used included a range of signal strengths in both rightward and leftward directions.

2.3. Procedure

Each experimental run commenced with an adaptation period lasting 56 s (14 cycles of the 4-s sequence described above). This was followed by the first test trial, which lasted 0.43 s. Further test trials then followed, separated by top-up adaptation lasting 4 s. A brief (100 ms) interval in which the screen was blank (luminance equal to the background luminance of the pattern) served to demarcate the adaptation and test intervals. The level of motion coherence of the test pattern varied from trial to trial within the run, according to the method of constant stimuli. Nine coherence levels were chosen ranging from 16% coherence leftward through zero to 16% rightward. Each level was presented ten times. The task of the subject was to indicate whether motion was rightward or leftward by pressing one of two buttons. Five such runs of 90 trials were completed, giving a total of 50 trials per coherence level. This procedure was repeated for each of the three adaptation conditions (leftward, rightward and balanced).

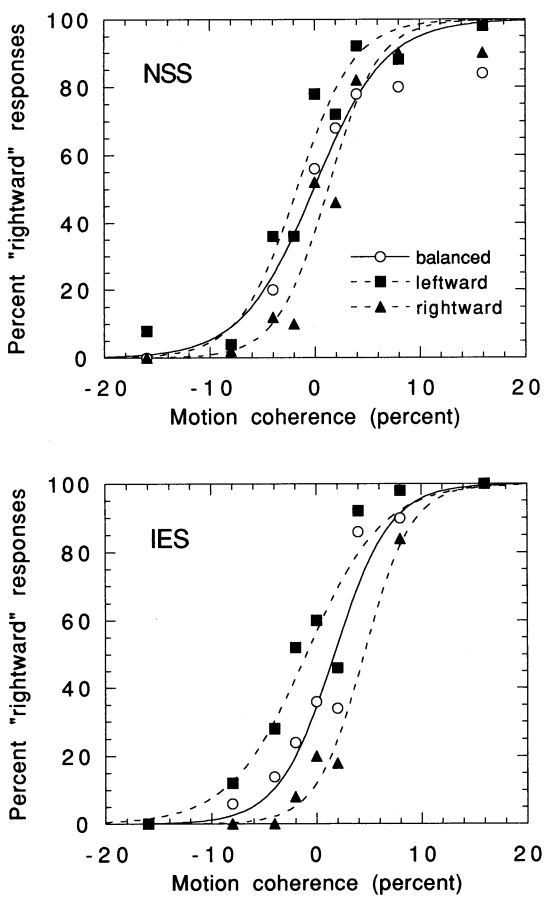

Fig. 1. Psychometric functions for the three adaptation conditions used in Experiment 1. Positive motion coherence values indicate rightward motion, negative values leftward motion. The symbols are empirical data points and the lines are best-fit sigmoid functions (constrained to asymptote at 0 and 100%). Results are shown separately for two observers.

For each condition, a psychometric function was plotted relating the percentage 'rightward' responses to the motion coherence level. A sigmoid function was fitted to the data using a least-squares method. The 50% point on this function indicates the coherence level at which the subject was equally likely to respond 'rightward' or 'leftward'. This point is expected to lie at 0% coherence without adaptation or with balanced adaptation.

2.4. Results and discussion

The results are shown separately for the two subjects in Fig. 1. In all three adaptation conditions, psychometric functions of the expected form were obtained. In the balanced adaptation condition (solid line), the function passes through the 50% point at a coherence level close to zero. The function for leftward adaptation is shifted leftwards, reflecting a greater proportion of 'rightward' responses and a midpoint at a non-zero, leftward coherence level. Similarly, the function for rightward adaptation is shifted to the right. The shift is small, but consistent across the observers. The size of the shift is plotted in Fig. 2a. These shift values reflect the deviation of the mid-point of the best-fit sigmoid function from zero coherence. Subject NSS shows a shift very close to zero in the balanced condition and symmetrical shifts in opposite directions in the other two conditions. Subject IES shows a similar pattern of results but with an overall bias in favour of 'leftward' responses.

The results demonstrate the existence of an aftereffect of adaptation. Rightward global motion adaptation results in a bias towards perception of leftward motion in the test pattern and vice versa. This shift cannot be attributed to the standard motion aftereffect, reflecting adaptation in local motion sensors, since local motion during adaptation is equal in the leftward and rightward directions. The direction bias resulting from adaptation is modest, but it must be remembered that the global motion percept during adaptation is quite weak.

3. Experiment 2

An alternative explanation of the after-effects of adaptation seen in Experiment 1 might be that although local motion is equal in opposite directions during adaptation, it is more visible in one direction than the other because of masking. The many additional noise dots that are present during signal motion in one direction might, as well as making global motion invisible, reduce the effectiveness of local motion in that direction as a physiological stimulus. This might reduce the level of adaptation that results from exposure to that direction. Experiment 2 was conducted in order to evaluate this interpretation of the results.

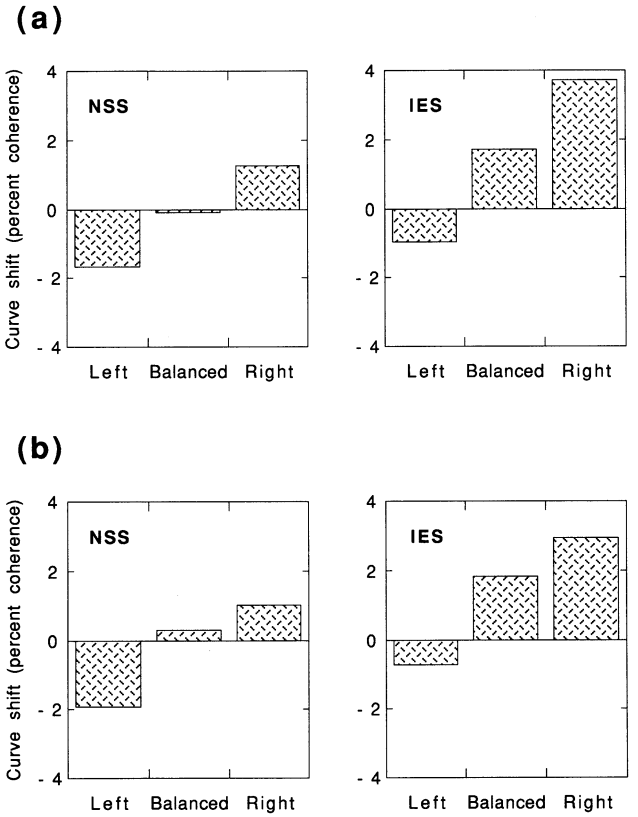

Fig. 2. Histograms showing the deviation (shift) of the midpoint of the psychometric function from zero coherence. Positive numbers on the ordinate indicate a rightward shift of the function (reflecting a bias towards perception of leftward motion), negative numbers indicate a leftward shift. (a) Results of Experiment 1. (b) Results of Experiment 2. Results are shown separately for the two observers in both cases.

3.1. Subjects

The subjects were the same as in Experiment 1.

3.2. Stimuli

The effects of a moving mask on sensitivity to motion are tuned for mask direction, being maximal when mask and probe directions are the same and falling off rapidly as they diverge (Anderson & Burr, 1985). Adaptation studies suggest that direction sensors are broadly tuned for direction, having a bandwidth of about $\pm 45°$ (Levinson & Sekuler, 1980). Consequently, it is possible to reduce or eliminate masking effects of noise dots on signal dots by constraining the directions of the noise dots so as to avoid directions close to the signal direction. This must be done without introducing an overall directional bias in the noise. To achieve this, the adaptation stimulus was again a four-frame sequence repeated many times. There were again three versions, rightward, leftward and balanced. The signal dots were the same as in Experiment 1, that is 25 dots moving alternately rightward and leftward. To these were added 22 noise dots with random directions. These were present in both adaptation phases (rightward and leftward signal dots). In the rightward adaptation case, a further 180 noise dots were added when the signal dots moved leftwards, to reduce or eliminate global motion. These were equally distributed among just four directions, namely the two opposite directions of motion along each of the two oblique axes midway between horizontal and vertical. Thus, the noise directions remained balanced, but no noise dots had directions within 45° of the signal dots (except the 22 that were present in both direction phases). The adaptation pattern again appeared as weak, continuous global motion and had a very similar appearance to that used in Experiment 1. The leftward adaptation stimulus was the same but with the directions reversed. The balanced adaptation pattern had 22 signal dots, 22 noise dots with random directions and 203 noise dots moving on the oblique axes; all were present in both signal direction phases.

3.3. Procedure

The procedure was identical to that of Experiment 1 except that the new versions of the three adaptation stimuli were employed.

3.4. Results and discussion

The psychometric functions obtained are shown in Fig. 3. They are similar in all respects to those obtained in Experiment 1 (Fig. 1). Fig. 2b shows the results in terms of the magnitude of the shift in perceived direction caused by adaptation. Again, they are similar to those of Experiment 1 (Fig. 2a). The shifts are still present, and there is no sign that they are reduced in magnitude.

This suggests that the shifts do not reflect a local motion imbalance induced by masking. However, the likely effect of additional noise dots is a rather complex issue from a theoretical perspective. Dots that are very close in direction can be expected to enhance, rather than reduce, the signal strength because they will fall within the sensitivity of neurones that are optimally sensitive to the signal direction. Dots with more remote directions can be expected to mask the signal dots due to inhibition between different directions. It is difficult to say over what range of dot directions the latter effect operates. Masking studies (e.g. Anderson & Burr, 1985) suggest a range of about $\pm 45°$, but the figure may be greater. Using an adaptation paradigm, Greenlee and Magnussen (1988) found inhibitory influences across orientations that peaked at 45° but were still in evidence up to about 70°. This experiment used static patterns, but raises the possibility of broadly tuned interactions among direction channels. For these rea-

sons, it is likely that local masking of the signal dots was not completely eliminated in Experiment 2.

A further qualification to be made is that it has been suggested that all directions are combined to produce a contrast normalisation signal (Simoncelli & Heeger, 1998). If this is correct, Experiment 2 does not provide an adequate control for the effect of the additional noise dots used in Experiment 1 to mask global motion. Inhibition due to contrast gain control will simply reflect the total number of dots, which is unequal for the two directions of motion in our adaptation stimuli. Constraining the directions of the additional noise dots will have no effect on the contrast normalisation signal. However, pooling across all directions is simply a convenient computational strategy and it remains to be seen whether physiological evidence will support it.

Overall, it seems unsafe to assume that Experiment 2 provides a completely reliable control. But it does seem reasonable to suppose that a substantial reduction, at least, in the magnitude of the aftereffect is expected in Experiment 2 compared with Experiment 1 if the aftereffect is due to local masking, whereas no reduction at all is evident.

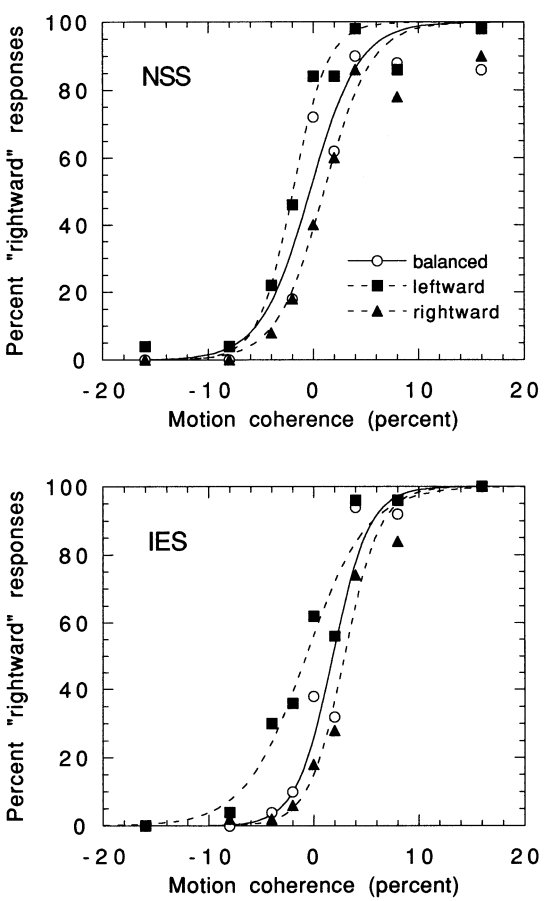

Fig. 3. Psychometric functions for the three adaptation conditions used in Experiment 2. Results are again shown separately for two observers.

4. Discussion

The results suggest that during exposure to global motion, adaptation occurs at the level at which global motion is represented. The anatomical location of this level is uncertain, although it is possible it is V5/MT, since lesions of this area in monkeys results in impairments in global motion perception (Newsome & Paré, 1988) and microstimulation of cells in this area can bias the perceived direction of global motion (Salzman, Britten & Newsome, 1990).

Comparatively little is known of the mechanisms of global motion perception. The existence of an adaptation procedure that isolates global effects may facilitate the clarification of such issues as the spatial extent over which motion integration occurs (Braddick, 1993), the spatial frequency specificity of the global motion system (Yang & Blake, 1994) and the role of second-order motion cues in global motion (Edwards & Badcock, 1995).

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